Hybridization between *Vachellia collinsii* and *V. pennatula* (Fabaceae: Mimosoideae) in the New World tropics

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ABSTRACT

Principal component analysis (PCA) and principal coordinate analyses (PCoA) suggests that *Vachellia collinsii* and *V. pennatula* occasionally hybridize. This putative hybrid shows a relationship to *V. collinsii* with some enlarged stipular spines that are rarely inhabited by ants, some leaflets with Beltian bodies, and usually 2 to 4 enlarged and cup-shaped petiolar glands. In contrast, the putative hybrid shows a relationship to *V. pennatula* with many pinna-pairs/leaf, numerous leaflets/pinna, small leaflets, and puberulent leaves. The hybrid between *V. collinsii* and *V. pennatula* (*Vachellia ×ziggyi*) is described.
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KEY WORDS: *Vachellia collinsii, V. pennatula,* Mimosoideae, hybridization.

The genus *Vachellia*, which includes the species of *Acacia* s.l. with paired stipular spines and flowers that lack a floral disc, consists of 60 species in the New World tropical and subtropical areas from southern United States south to Argentina (Seigler and Ebinger 2005). Also, nearly 100 additional species are found in the Old World tropics and subtropics of Asia, Africa, and Australia.

Hybrids between New Word *Vachellia* species are occasionally encountered. These hybrids mostly involve species belonging to the *Vachellia macracantha* species group that includes the ant-acacias and a few related taxa (Maslin and Stirton 1997, Ebinger and Seigler 1992, Seigler and Ebinger 1995). Hybrids between ant-acacia species and between ant-acacias and non-ant-acacias have been discussed by Janzen (1974), Ebinger and Seigler (1992), and Seigler and Ebinger (1995). These studies indicate that at least four ant-acacia species hybridize with various non-ant-acacia species including *V. campechiana* (Mill.) Seigler & Ebinger, *V. macracantha* (Willd.) Seigler & Ebinger, and *V. pennatula* (Schltdl. & Cham.) Seigler & Ebinger (Ebinger and Seigler 1987, Seigler and Ebinger 1988). The present study was undertaken to examine the morphological differences of probable hybrid individuals involving the ant-acacia species *V. collinsii* (Saff.) Seigler & Ebinger and a related non-ant-acacia species, *V. pennatula*. These two species are sympatric throughout much of Mexico and Central America, and are commonly associated with disturbance in thorn-scrub and ruderal communities.

MATERIALS AND METHODS

These analyses were based on herbarium specimens of the putative parents and hybrids from Mexico and Central America (Appendix I). Initially, the specimens were separated into taxonomic groups based on overall morphological similarity. These specimens were scored for 12 characters (Appendix II). These data served as the source of characters for principal components analyses (PCA) and principal coordinates analyses (PCoA). Three or more measurements were made for each continuous character of each specimen. These values were then plotted to confirm that gaps in the data exist.

A PCA to identify groupings of the specimens examined was carried out. For this analysis, the data were first standardized and a correlation matrix, eigenvalues, and eigenvectors were calculated using NTSYS-pc verson 2.1 (Rohlf 2000). Eigenvectors were scaled by the square root of λ. The axes were rotated and the resulting loading values graphically represented as both two- and three-dimensional plots.

To carry out the PCoA analysis, Gower's resemblance coefficients were calculated (Legendre and Legendre 1983, Podani 1999, Dickinson 2000). The nature of each character was designated as binary, multistate, or quantitative descriptors and all characters were weighted equally (Dickinson 2000). The data matrix was transformed by the DCENTER algorithm using distances squared and eigenvectors and eigenvalues calculated with NTSYS-pc verson 2.1 (Rohlf 2000). Eigenvectors were scaled by the square root of λ. The resulting loading values were graphically represented as both two- and three-dimensional plots (Figure 1).

RESULTS

The analyses involved 11 specimens of *Vachellia collinsii*, 11 specimens of V. *pennatula* and four probable hybrids. The PCA based on 12 characters (Appendix II), and a PCoA based on Gower's similarity coefficients for species scored proved to be similar (Figure 1). In the PCA, the first three principal components accounted for 96% of the total variance. Spine size (Ssi), Beltian bodies (Bbo), leaflet length (Lle) and pinna pair number (Ppn) (characters 1, 2, 9, and 5) were most important for determining the component score of the first axis; pinna length (Ple), leaflets/pinna (Lpi), petiole gland shape (Pgs), and leaflet pubescence (Lpu) (characters 6, 7, 4, and 12) were most important for determining the second axis. The specimens used in this analysis represented distinct groupings in both PCA and PCoA, the results showing that the parent species were well separated with putative hybrids located between them (Figure 1).

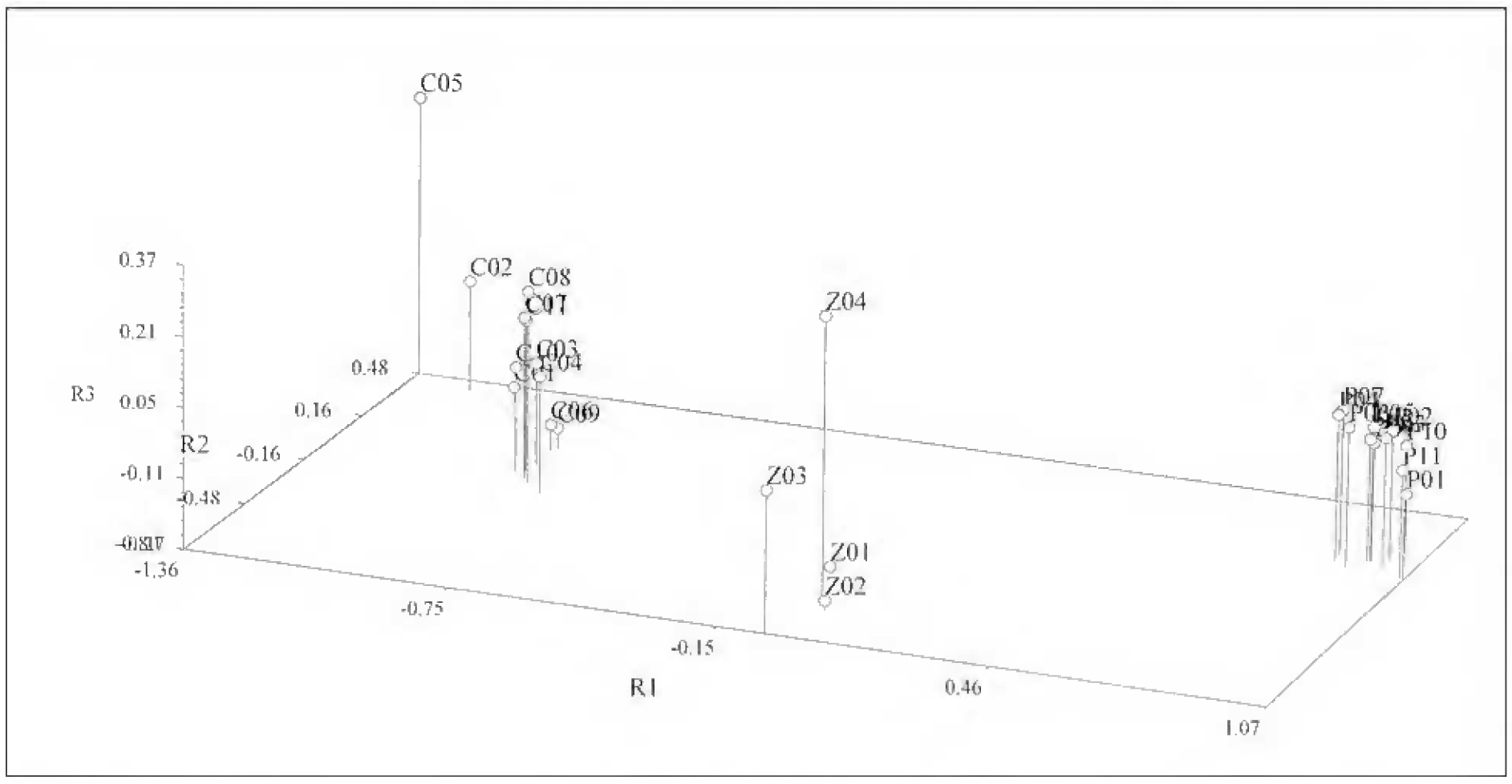

Figure 1. Plot of axis 1 v. 2 for the principal components analysis using the 12 characters (Appendix II) on 11 specimens of *Vachellia collinsii* (C01-C11), 11 specimens of *V. pennatula* (P01-P11), and four specimens of the probable hybrids (*V. x ziggyi*) (Z01-Z04).

DISCUSSION

Vachellia collinsii has the most extensive distribution of all ant-acacias, extending from central Mexico (states of Campeche, Chiapas, Durango, Guerrero, Nayarit, Oaxaca, Quintana Roo, and Yucatán), south through Central America into Colombia (states of Atlántico and Bolívar). The non-ant-acacia, *V. pennatula* has a similar, but more extensive distribution, extending from northern Mexico (states of Sonora and Tamaulipas) south through most of Mexico, through Central America, and into Colombia (state of Valle de Cauca) and Ecuador (states of Cotopaxi and Pichincha). The hybrid, in contrast, has a somewhat restricted range and appears to arise from occasional hybridization in areas where the two parental species overlap. Based on intermediacy in PCA analyses, all collections we have seen appear to be F_1–hybrids. We have only encountered specimens from Guatemala (state of Guatemala), Mexico (states of Chiapas and Oaxaca) and Nicaragua (states of Estelí and Madriz) (Appendix I).

The hybrid *Vachellia collinsii x V. pennatula* can easily be separated from both parent using many of the characteristics listed in Appendix I. The most obvious and commonly used characteristics include: occasional Beltian bodies on a few leaflets and occasional enlarged stipular spines on the hybrid that are absent in *V. pennatula* but common in *V. collinsii*; the presence of 2 to 5 broadly dome-shaped to volcano-shaped petiolar glands for *V. collinsii*, 2 to 4 enlarged and cup-shaped petiolar glands in the hybrid, while in *V. pennatula* the petiolar gland is solitary and flat; and leaflets that are larger in *V. collinsii* (6-13 mm long and 1.3-3.1 mm wide), smaller in the hybrid (2.0-4.5 *x* 0.8-1.1 mm), and much smaller in *V. pennatula* (0.8-3.0 *x* 0.4-0.7 mm). The proposed new hybrid is described, being named after a cartoon character affectionately called Ziggy.

Diagnosis: *Vachellia x ziggyi* Seigler & Ebinger differs from other *Vachellia* species in that it has alternate leaves 40 - 160 mm long, symmetrical stipular spines 10 - 40 x 2 - 6 mm near the base, 2-4 petiolar glands scattered along the petiole, and inflorescences densely-flowered spikes, 1.5 to 2 times longer than wide, in short racemose clusters.

Vachellia x ziggyi Seigler & Ebinger, **nothomorph nov.** (*Vachellia collinsii x V. pennatula*)

TYPE: MEXICO, Oaxaca. A 5 km al NE de San Pedro Tepanatepec, Distr. Juchitán, 200 m, 16 Dec 1978, *M. Sousa, L. Rico & P. Basurto 10157* (holotype: MO). (Figure 2)

Shrub or small **tree** to 5 m tall; bark not seen; twigs dark reddish brown, slightly flexuous, glabrous to lightly puberulent; short shoots absent; prickles absent. **Leaves** alternate, 40–160 mm long; stipular spines light to dark purple brown, symmetrical, terete to sometimes slightly flattened, straight, stout and inflated, 10–40 x 2–6 mm near the base, glabrous to lightly puberulent, some spines not enlarged, these usually less than 5 mm long; petiole adaxially grooved, 4–10 mm long, puberulent; petiolar glands (1)2 to 4, scattered along the petiole, sessile, enlarged and cup-shaped, apex circular oblong and depressed, base 1.1–2.5 mm long, sometimes the glands overlapping and continuous, puberulent; rachis adaxially grooved, 30–150 mm long, puberulent, glands absent to sometimes present between the upper 3 to 5 pinna pairs; pinnae 6 to 20 pairs per leaf, 15–40 mm long, 4–9 mm between pinna pairs; paraphyllidia absent; petiolules 0.4–0.9 mm long; leaflets 12 to 33 pairs per pinna, 0.5–1.2 mm between leaflets, linear, 2.0–5.2 x 0.8–1.2 mm, glabrous to lightly puberulent, lateral veins not obvious, only one vein from the base, base oblique, margins lightly ciliate, apex obtuse; Beltian bodies rare, usually only on the lower few leaflets of some pinna. **Inflorescence** a densely-flowered subglobose spike about 1.5 to 2 x longer than wide, 9–15 x 6–8 mm, in short racemose clusters to 50 mm long with 1–4 spikes per node in each of the 2 to 4 nodes; peduncles 10–25 x 0.8–1.6 mm, densely puberulent; receptacle slightly enlarged; involucre 3- to 5-lobed, located just below the spike, persistent; floral bracts stalked, 1.0-1.5 mm long, apex oval, ciliate, deciduous. **Flowers** sessile, yellow; calyx 5-lobed, 0.8–1.3 mm long, glabrous to lightly puberulent; corolla 5-lobed, 1.4–1.8 mm long, lobes less than one-quarter the length of the corolla,

glabrous; stamens 40 to 60; stamen filaments 2.0–3.3 mm long, distinct; anther glands absent; ovary glabrous, sessile. **Legumes** not seen. **Seeds** not seen.

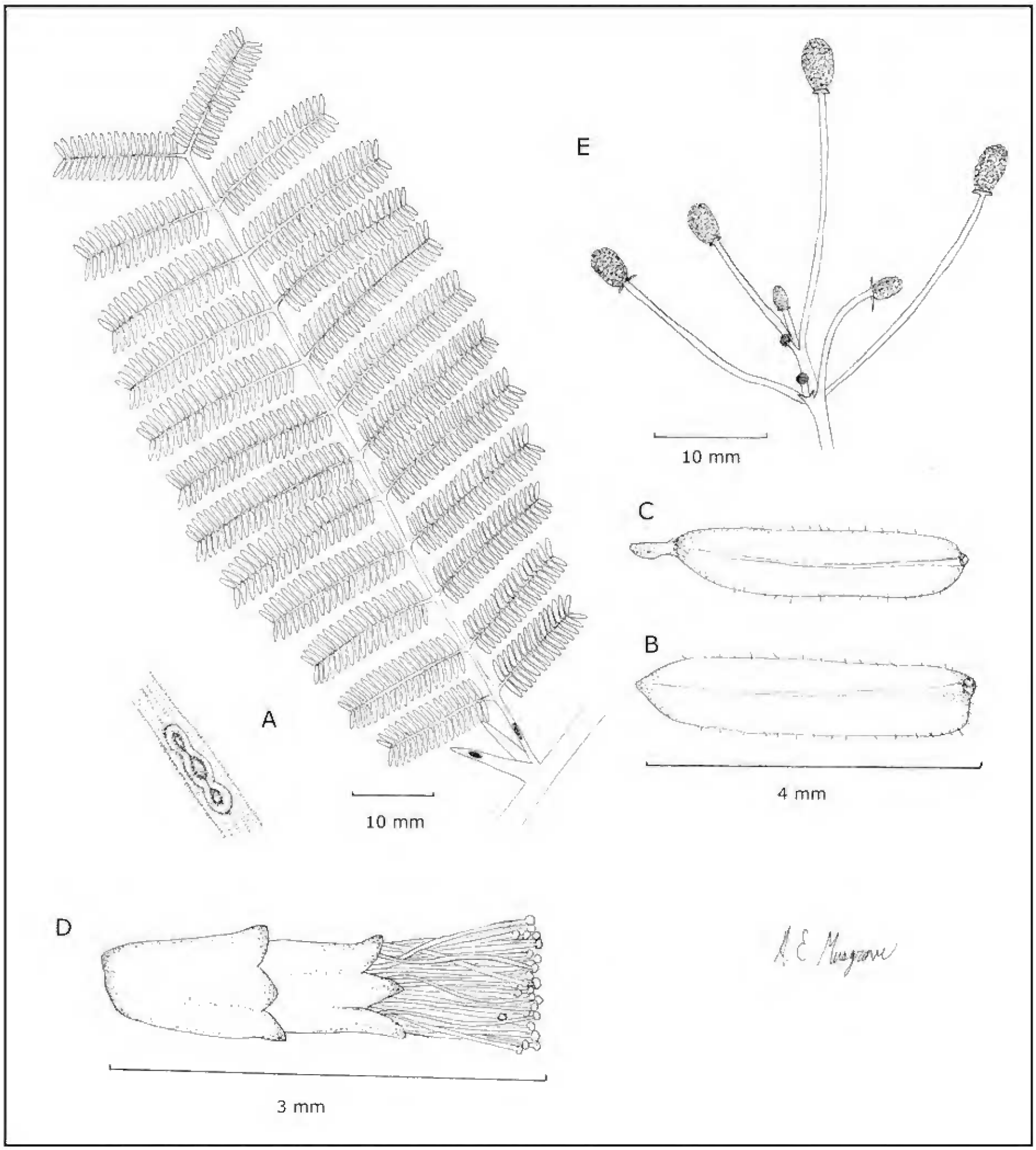

Figure 2. *Vachellia x ziggyi* Seigler & Ebinger, A: Leaf with petiolar glands and stipular spines including an entrance made by ants (*Janzen 571*), B: Leaflet (adaxial surface) (*Janzen 571*). C: Leaflet with incompletely-formed Beltian body (*Janzen 571*). D. Flower (*Sousa et al. 10157*). E. Racemose pseudo-inflorescence with immature subglobose inflorescences (*Sousa & Rico 10157*).

The puberulent stipular spines, petioles, and rachises of these hybrids suggest that *Vachellia pennatula* is the non-ant-acacia parent. Also, the young leaves are densely puberulent, a characteristic of young leaves of *V. pennatula.* The enlarged stipular spines, the presence of Beltian bodies on the lower 1 to 2 leaflets of some pinna pairs, and the broadly dome-shaped petiolar glands indicate *V. collinsii* as the probable ant-acacia parent. The one flowering specimen observed (*M.Sousa et al. 10157*) indicated a relationship to *V. collinsii* with subglobose inflorescences in short racemose clusters. On some herbarium specimens, the collector (Dr. Daniel H. Janzen) mentioned that *V. collinsii* was the only ant-acacia present at the site.

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APPENDIX I. Specimens examined for PCA and PCoA analyses involving *Vachellia collinsii, V. pennatula*, and the putative hybrid (*V. x ziggyi).*

Vachellia collinsii (Safford) Seigler & Ebinger: **COLOMBIA: Bolívar:** Arenal, 45-60 m, 22 Apr 1966, *E.Forero G. & R.Jaramillo M. 496* (EIU); Cartagena, 7 km SW of Arroyo Grande, 70 m, 31 Jul 1985, *J.L.Zarucchi & H.Cuadros 3902* (ILL). **COSTA RICA: Guanacaste:** La Pacifica, near Cañas, 28 Jul 1985, *D.S.Seigler 12269* (ILL); Finca La Pacifica, near Duck Pond, 15 Aug 1985, *D.S.Seigler 12367* (ILL). **MEXICO: Campeche:** 13 miles SW of Champotón Bridge, route 180, 5 Jun 1980, *D.S.Seigler, P.M.Richardson & S.Thompson 11606* (ILL); 13 miles SW of Champotón Bridge, route 180, 5 Jun 1980, *D.S.Seigler, P.M.Richardson & S.Thompson 11607* (ILL). **Oaxaca:** 30 km E of Puerto Escondido, route 200, 18 Jul 1993, *D.S.Seigler, D.Clarke & K.Potgieter 13930* (ILL). **Quintana Roo:** 51 miles S of Valladolid, Yucatán, route 295, 3 Jun 2005, *D.S.Seigler & B.R.Maslin 16038* (ILL). **Yucatán:** Chichén Itzá, 4 Jun 1980, *D.S.Seigler, R.M.Richardson & S.Thompson 11599* (ILL). **PANAMA: Panama:** 1 km E of Chorrera City limits. 30 May 1977, *J.P.Folsom 3464* (ILL). **Los Santos:** Vicinity of Tonosí, 26 Feb 1963, *W.L.Stern, R.H.Eyde & E.S.Ayensu 1831* (ILL).

Vachellia pennatula (Schltdl. & Cham.) Seigler & Ebinger: **GUATEMALA: Guatemala:** 19 km S of Guatemala City, route 8, 1 Sep 1965, *D.H.Janzen 776* (ILL). **MEXICO: Morelos:** 3 km N of Alpuyeca, route 95, 19 Nov 1985, *D.S.Seigler & J.E.Ebinger 12607* (ILL). **Jalisco:** 12 miles NW of Tecolotlán, route 80, 21 Jul 1975, *D.S.Seigler & G.Holstein 9533* (ILL). **Oaxaca:** 39 miles W of Tehuantepec, route 190, 8 Aug 1966, *D.H.Janzen 605* (ILL); 46.7 miles W of Tehuantepec, route 190, 10 Jan 1965, *D.H.Janzen 757* (ILL); 10 km SE of Matatlán, route 190, 19 Jul 1993, *D.S.Seigler, H.D.Clarke & K.Potgieter 13955* (ILL); 11 miles SE of Huahuapan de León, route 180, 28 May 2005, *D.S.Seigler, J.Miller & B.R.Maslin 15989* (ILL); **Puebla:** Near Izúcar de Matamoros, route 160, 5 Jul 1986, *D.S.Seigler & B.Maslin 12685* (ILL). **Veracruz:** 12 miles W of Conejos on road to Huatusco, 26 Apr 1964, *D.H.Janzen 723* (EIU); 1 mile E of Actopan, route 140, 18 Nov 1985, *D.S.Seigler & J.E.Ebinger 12540* (EIU); 23.4 miles W of El Tamarindo, route 140, 16 Sep 1984, *D.S.Seigler, S.Berlocher & D.Nickrent 12231* (ILL).

Vachellia x ziggyi Seigler & Ebinger: **GUATEMALA: Guatemala:** 16.2 miles NE of Guatemala City, road to Puerto Barrios, 14 May 1965, *D.H.Janzen 744* (EIU, ILL), *745* (EIU, MO), *746* (EIU, MO), *747* (EIU, MO). **MEXICO: Chiapas:** Suckers from cut stump, pasture, 8.5 miles S of La Trinitaria, route 190, 1160 m, 7 Aug 1966, *D.H.Janzen 572* (EIU), *573* (EIU), *574* (EIU). **NICARAGUA: Estelí:** 15.8 miles W of Sebaco, 550 m, 11 May 1976, *D.H.Janzen 742* (EIU). **Madriz:** 2.5 miles SW of Somoto, 11 May 1965, *D.H.Janzen 737* (EIU), *738* (EIU).

APPENDIX II. Characters scored for principal component (PCA) and principal coordinate analyses (PCoA) for the *Vachellia collinsii/pennatula* complex.

1. Spine size (Ssi) 1 = enlarged, mostly inhabited by ants, 2 = slightly enlarged, mostly not inhabited by ants, 3 = not enlarged nor inhabited by ants.
2. Beltian bodies (Bbo) 1 = present on many leaflets, 2 = restricted to a few leaflets on lower pinna, 3 = absent.
3. Petiole gland number (Pgn) 1 = glands 2-5 per petiole, 2 = solitary.
4. Petiole gland shape (Pgs) 1 = domed-shaped; 2 = flattened.
5. Pinna pair number (Ppn).
6. Pinna length near middle of leaf (mm) (Ple).
7. Leaflets/pinna (Lpi).
8. Leaflets, distance between (mm) (Ldb).
9. Leaflet length (mm) (Lle).
10. Leaflet width (mm) (Lwi).
11. Leaflet venation (Lve) 1 = lateral veins obvious, 2 = lateral veins not obvious.
12. Leaflet pubescence (Lpu) 1 = glabrous or nearly so, 2 = puberulent.